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Carbon Budgets for Two Species of Benthonic Symbiont-Bearing Foraminifera

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Abstract. Carbon budgets are presented for two symbiont-bearing foraminifera: *Amphistegina lobifera*, a perforate species, and the imperforate species *Amphisorus hemprichii*. Both species have a potential for autotrophy with respect to carbon, because the translocation from symbionts to host is sufficient to account for the increase in measured biomass. Experimentally determined feeding rates exceed the supposed amount of food retained as calculated by balancing the budget by a factor of up to ten. When feeding does not occur, the carbon budget of *A. lobifera* is almost exactly balanced, whereas the budget of *A. hemprichii* can be balanced within the precision of the measurements. Carbon for calcification by *A. lobifera* is initially concentrated in an internal pool that derives approximately 10% of its content from organic matter respired by the host. Carbon of organic origin was not incorporated into the skeleton of *A. hemprichii*.

Introduction

Carbon budgets have been constructed for various invertebrates bearing algal symbionts, such as corals (Muscatine *et al.*, 1981, 1984; Falkowski *et al.*, 1984) and zoanthids (Steen and Muscatine, 1984), but not for foraminifera. One of the reasons for this is that carbon budgets can only be formulated once the flows of carbon and the mechanisms involved in directing these flows are known qualitatively. Then a scheme integrating all fluxes can be drawn up, so that research aimed at quantifying these fluxes can be properly interpreted. Earlier research within this framework showed that the perforate and imperforate groups of foraminifera have widely different mechanisms for uptake of inorganic carbon and for calcification (ter Kuile and Erez, 1987, 1988; ter Kuile *et al.*, 1989). Therefore, two conceptually different budgets must be constructed for foraminifera: one for a representative of the perforate, and one for an imperforate species. The species we have chosen for this study are: *Amphistegina lobifera* (perforate) and *Amphisorus hemprichii* (imperforate).

In earlier studies on carbon budgets of symbiont-bearing calcifying systems, the contribution of the symbionts to the carbon requirements of the host was considered a key feature of the host-symbiont relationship and was, therefore, often emphasized. Determination of the carbon translocation from symbionts to host is difficult because it involves measurements within an organism. Another disputed parameter is the relative contribution of feeding to the carbon requirements of the host. Lee and coworkers (Lee and Bock, 1976; Lee *et al.*, 1980) estimated that, in foraminifera, carbon from feeding exceeds carbon from photosynthesis by a factor of 10, but ter Kuile *et al.* (1987) found a ratio of 0.5–2. Feeding rates are difficult to measure because feeding is episodic, and because egested algae do not resuspend well. At least in foraminifera, feeding seems to provide nutrients rather than carbon (ter Kuile *et al.*, 1987). Hence, minimum feeding rates can be estimated by calculating the nutrient requirements of the host symbiont-system by assuming a constant ratio of carbon to nutrients. One purpose of this study is to estimate the two uncertain parameters: translocation of carbon from symbionts to host, and the contribution of feeding to the carbon budget. The calculated values, estimated by balancing the budget so that no carbon is unaccounted for,

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are used as a control on the experimentally obtained values.

Based on stable isotope experiments with corals and foraminifera, Goreau (1977) and Erez (1977, 1978) suggested that inorganic carbon is initially taken up in an internal inorganic carbon pool. According to this view, some respired carbon of organic origin may be taken up by the inorganic pool and afterwards incorporated into the skeleton. Later, experimental evidence was found for the existence of the inorganic carbon pool in perforate, but not in imperforate foraminifera (ter Kuile and Erez, 1987, 1988). Such pools have not been included in the earlier proposed budgets for corals (Falkowski *et al.*, 1984). We believe, however, that the internal inorganic carbon pool is important for overall carbon cycling, at least in perforate foraminifera. Therefore, the second purpose of this study is to understand the role of the pool in the carbon cycling of the perforate species.

The following observations have to be taken into account while formulating carbon budgets for foraminifera. First, the important taxonomical differences between the perforate and imperforate groups of foraminiferal species are reflected in widely different calcification mechanisms (ter Kuile *et al.*, 1989). Therefore two different models are proposed, one for each group.

Perforate species

Inorganic carbon (Ci) is initially taken up from seawater in one flow in the form of bicarbonate. In the cytoplasm, CO_2 is photoassimilated by the symbionts, and $CO_3^=$ is concentrated in the internal inorganic carbon pool (hereafter called "pool"), which serves for calcification only and not for photosynthesis. About 10% of the carbon incorporated into the skeleton consists of carbon originally photoassimilated by the symbionts and respired by the host. Feeding seems to provide nutrients, phosphate and nitrogen compounds, rather than carbon, to the host-symbiont system. (Leutenegger, 1977; Leutenegger and Hansen, 1979; ter Kuile and Erez, 1987, 1988; ter Kuile *et al.*, 1987, 1988, 1989).

Imperforate species

Inorganic carbon is taken up from seawater in two separate flows that do not interfere with each other. Carbonate is taken up by a diffusion-limited process into vacuoles where calcification occurs. The symbionts use either CO_2 or HCO_3^-. Some carbon derived from feeding may be assimilated in the host organic matter, but not in the skeleton. Internal recycling of respired carbon from organic origin into the skeleton does not occur (Hemleben *et al.*, 1986; ter Kuile and Erez, 1987, 1988; ter Kuile *et al.*, 1987, 1989).

We present carbon budgets for two species of foraminifera, based on rates determined in a large number of experiments; some of the data were obtained from other studies (ter Kuile and Erez, 1987, 1988; ter Kuile *et al.*, 1987).

Materials and Methods

Amphistegina lobifera (perforate) and *Amphisorus hemprichii* (imperforate) were collected from *Halophila* sp. plants, 24 h before each experiment. We checked the foraminifera for viability by observing their overnight upward mobility in glass jars (ter Kuile and Erez, 1984, 1987). The budget presented for *A. lobifera* comprises measurements of specimens with average weights of 66 to 72 μg (Table I); specimens of *A. hemprichii* weighed 385 μg on average, ranging from 242 to 523 μg. Long-term kinetic and pulse-chase experiments involving ^{14}C tracer techniques (ter Kuile and Erez, 1987, 1988) were used throughout the study. Incubations were carried out in 100 ml erlenmeyer flasks near a north-oriented window in natural light/dark cycles. The maximum light intensity was 750 $\mu E\ m^{-2}s^{-1}$, which corresponds to a depth of 15 m, similar to the depth of the sample location. Twenty to 40 mg of organisms were used for each incubation.

Determination of compartment biomass

The biomass of the following compartments was measured: total dry weight, biomass of the organic matter, dry weight of the skeleton, and the carbon content of internal inorganic carbon pool. Determinations of protein and chlorophyll content were used to estimate symbiont biomass.

Total dry weight of foraminifera was determined with a Cahn 25 electrobalance. Biomass of organic matter was measured as the additional weight of a Nuclepore (0.4 μ) filter on which the particulate organic matter of a sample whose shell was dissolved in 8.5% H_3PO_4 had been collected. The organic matter of *Amphistegina lobifera* was, on the average, 8.0% ($\pm$0.6, n = 48) of the total dry weight, and *Amphisorus hemprichii* contained 5.2% ($\pm$0.6) organic matter. The dry weight of the skeleton was determined by substracting the dry weight of the organic matter from the total dry weight. The internal inorganic carbon pool size of *A. lobifera* was measured by ^{14}C radiotracer methods, in combination with pulse-chase experiments (ter Kuile and Erez, 1988).

The protein content of finely crushed, dried specimens was determined by the Lowry method, as modified by Peterson (1977). The contribution of the symbionts to the organic matter could be estimated from the chlorophyll content measured after extraction in methanol (Strickland

and Parsons, 1972); this was possible because we found no change in the chlorophyll to protein ratio in samples obtained at depths less than 35 m. Sizes of compartments are given in μg C/mg foram (total dry weight of skeleton and organic matter).

Fluxes between the compartments

The following five fluxes were measured; the methods used were exactly those of the papers cited in each case. (1) The uptake of inorganic carbon from the medium—consisting of photoassimilation, uptake into the skeleton, uptake into the pool and, by addition, total uptake—was measured as $H^{14}CO_3^-$ uptake (ter Kuile and Erez, 1987, 1988). (2) Translocation of photosynthates from symbionts to host was calculated from pulse-chase experiments (ter Kuile and Erez, 1987). (3) Incorporation of metabolic carbon (initially taken up photosynthetically) into the skeleton was also derived from pulse-chase experiments, (ter Kuile and Erez, 1987, 1988). (4) Respiration was again derived from pulse-chase experiments. (5) Uptake and rejection of carbon derived from feeding on algae in the environment (not their own symbionts) was determined in time-course and pulse-chase experiments as previously reported (ter Kuile *et al.*, 1987). All rates are given in μg C/mg foram/24 h in a natural light/dark cycle.

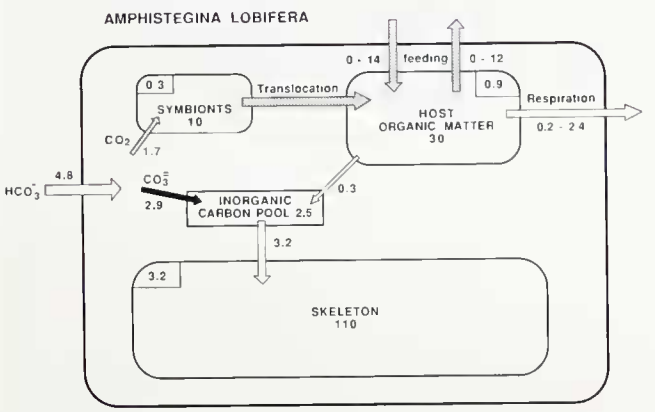

Figure 1. Carbon budget for *Amphistegina lobifera*. The compartments and the fluxes between them were qualitatively described in earlier studies (see Introduction). The names and sizes of different compartments are given in large letters and numbers; the names of processes and the amounts of carbon transferred are in small lettering. Open arrows indicate transfer of inorganic carbon, striped arrows indicate transfer of organic carbon, and closed arrows indicate the active transport of carbonate. Numbers framed in compartment corners indicate daily increase in size of that compartment. Units: sizes of compartments in μg C/mg foram. Rates of fixation and transfer, and daily increase, in μg C/mg foram/24 h in a natural light/dark cycle.

Table I

Rates of carbon fixation and pool size in Amphistegina lobifera *in a natural light/dark cycle*

Org. wt. (μg)	Total	Photo	Skeleton	Pool size (μg C/mg foram)
	(μg C/mg foram/24 h)			
66	4.9	2.0	2.9	
68	4.8	1.6	3.2	2.5[a]
68	5.1	1.7	3.4	
70	5.5	1.9	3.6	
72	3.9	1.2	2.7	
	—	—	—	
Average:	4.8	1.7	3.2	

[a] In experiments not reported here, a pool size of 2.2 to 2.9 μg C/mg foram was measured in foraminifera with an organism weight of about 70 μg.

Abbreviations: Org. wt = organism weight; Total = total carbon uptake; Photo = carbon uptake for photosynthesis by the symbionts; Skeleton = carbon uptake for calcification; Pool size = carbon content of the internal inorganic carbon pool for calcification. The standard deviation of a large number of measurements on identical samples, which were made using our methodology, was around 5% of the reported value (ter Kuile and Erez, 1987).

Results

Budget descriptions

The carbon budget for *Amphistegina lobifera* is presented in Figure 1. The compartments are defined and their size determined as described above in Materials and Methods. The existence of the fluxes between them was demonstrated in earlier studies (ter Kuile and Erez, 1987, 1988; ter Kuile *et al.*, 1989, see Introduction). The uptake rates used to construct the budget are given in Table I. The organic compartment makes up 8.0% of the total dry weight. About half of organic dry weight is carbon (Sverdrup *et al.*, 1942; Parsons and Takahashi, 1973), which amounts to 40 μg C/mg foram. The ratio of chlorophyll to protein is roughly 1:39 (Table II); a usual ratio for algae is 1:10 (Parsons and Takahashi, 1973). Thus, the symbionts comprise about one quarter of the total organic matter. The organic matter compartments of symbionts and host contain about 10 and 30 μg C/mg foram, respectively. The skeleton comprises 92% of the total dry weight, which amounts to 110 μg C/mg foram. The inorganic carbon pool size (ter Kuile and Erez, 1988) depends on the calcification rate, which in turn depends on the size of the specimens. For specimens of roughly 70 μg, a pool size of approximately 2.5 μg C/mg foram (Table I) was found in the experiments performed for this study. In other studies we found similar values (2.2–2.9 μg C/mg foram) (ter Kuile and Erez, 1988).

Total uptake of inorganic carbon (Ci) by *Amphistegina lobifera* was, on average, 4.8 μg C/mg foram/24 h (Table

Table II

Protein and chlorophyll measurements of Amphistegina lobifera *and* Amphisorus hemprichii *(duplicate measurements on different size groups)*

	Protein (μg/mg foram)	Organism weight (μg)
A. lobifera	33.92	340
	32.10	340
	40.05	60
	39.40	60
A. hemprichii	20.88	1107
	17.10	1107
	26.30	283
	23.49	283
	Ratio protein/ chlorophyll (μg/μg)	**Organism weight (μg)**
A. lobifera	39.7	>250
	37.4	75–250
	40.1	<75
A. hemprichii	45.2	>2000
	34.7	>2000
	40.8	<500
	41.4	<500

1). Under the experimental conditions, specimens of the size range used in this study (around 70 μg) grew at a daily rate of about 3%/day. This rate was determined optically, by converting size increase to weight increase (ter Kuile and Erez, 1984), and by the incorporation of $^{14}CO_3^{2-}$ into the skeleton. Approximately 1.7 (1.2–2.0) μg C/mg foram/24 h net is fixed photosynthetically by the symbionts. The chlorophyll:protein ratio does not change with size (Table II), indicating that the symbionts grow in proportion to the organic matter. When growing at a rate of 3% a day, the symbionts need 0.3 μg C/mg foram/24 h for growth. Hence, a net amount of 1.4 μg C/mg foram/24 h will be available for translocation to the host. Calculations based on the results of pulse-chase experiments indicate a transfer of 1.3 μg C/mg foram/24 h. At the measured growth rate, the host needs 0.9 μg C/mg foram/24 h for growth. Transfer of respired Ci to the skeleton amounts to 0.3 μg C/mg foram/24 h. Loss of respired Ci to the environment is roughly 0.2 μg C/mg foram/24 h. Incorporation into the skeleton is 3.2 μg C/mg foram/24 h (Table I). This carbon is initially concentrated in the pool which, in turn, derives 0.3 μg C/mg foram/24 h from respired carbon (see above) and, by balance, 2.9 μg C/mg foram/24 h is taken up directly from seawater. When no feeding occurs, the budget is balanced with respect to uptake, growth, and respiration. During feeding experiments, large amounts of labeled algae (up to 14 μg C/mg foram/24 h) were rapidly ingested, but most of this food was egested in organic form within 24 h (ter Kuile *et al.*, 1987). Approximately 8% of the carbon in the food was respired. Less than 2% of the label taken up through feeding was incorporated into the skeleton (ter Kuile *et al.*, 1987). Feeding rates depend on the conditions during preincubation and the availability of suitable food. Therefore, the values given in Figure 1 must be considered minimum and maximum rates, rather than long-term averages. Consequently, the value for respiration is at a minimum when no feeding occurs and organisms grow slowly, and at a maximum when feeding rates, and thus growth rates, are high.

Amphisorus hemprichii *budget*

A similar budget for the carbon cycling of *Amphisorus hemprichii* is presented in Figure 2. This budget differs strongly, not only quantitatively, but qualitatively as well, from the budget of *A. lobifera*, reflecting the widely different calcification mechanisms found in perforate and imperforate foraminifera, respectively (see Introduction). Because of the large size range, the variation in the data was also large (Table III). The organic matter was 5.2% of the total weight (dry weight/dry weight). Symbiont biomass is about one quarter of the total organic matter, estimated from the chlorophyll:protein ratio (1:40.5 ± 4.3; ter Kuile and Erez, 1984; this study, Table II). When converted to carbon weight, the sizes of the organic compartments are 7.5 μg C/mg foram for symbionts, and 22.5 μg C/mg foram for the host. Skeleton contains 113 μg C/mg foram. *A. hemprichii* does not contain an internal inorganic carbon pool for calcification (ter Kuile and Erez, 1987, 1988).

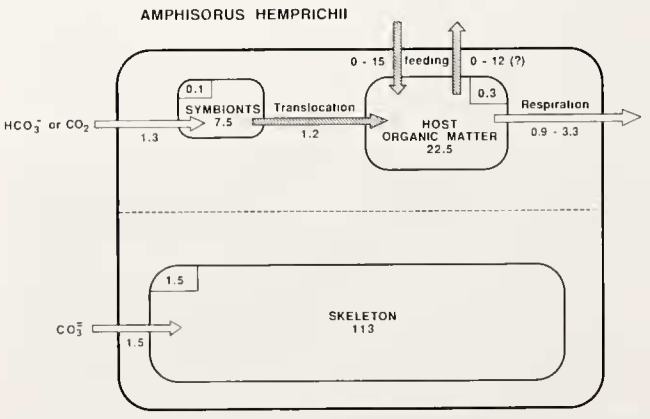

Figure 2. Carbon budget for *Amphisorus hemprichii*. This budget differs from that of *Amphistegina lobifera* due to differences in the calcification mechanisms (see Introduction). Units as in Figure 1.

Table III

Rates of carbon fixation in Amphisorus hemprichii *in a natural light/dark cycle. No internal inorganic carbon pool is observed in* A. hemprichii

Org. wt. (μg)	Total	Photo (μg C/mg foram/24 h)	Skeleton
243	2.5	1.5	1.0
362	2.9	1.1	1.8
409	2.5	1.0	1.5
523	3.7	1.7	2.0
	—	—	—
Average *	2.9	1.3	1.6
116	3.3	1.2	2.1
149	3.0	1.2	1.8
3000	2.2	1.3	0.9
3500	2.8	1.6	1.2

* Light and heavy specimens, not used in Figure 2.
Abbreviations and units as in Table I.

In the experiments for this budget, a net average of 1.3 μg C/mg foram/24 h (Table III) was fixed photosynthetically. Because *Amphisorus hemprichii* grew roughly 1.5%/day in the laboratory (ter Kuile and Erez, 1984, 1987), the symbionts and the host organic matter compartments increase 0.1 and 0.3 μg C/mg foram/24 h, respectively. By balance, 0.9 μg C/mg foram/24 h should be respired. The respiration rate calculated from pulse-chase experiments (ter Kuile and Erez, 1987) was 1.1 μg C/mg foram/24 h. Translocation, estimated from pulse-chase experiments, was 1.5 μg C/mg foram/24 h. The calculated rate is 1.2 μg C/mg foram/24 h, which is within the precision of the measurement. Up to 15 μg C/mg foram/24 h is taken up through feeding (ter Kuile *et al.*, 1987). In one pulse-chase experiment, 25% of the amount initially ingested was still present after one week. Thus, feeding may contribute considerable amounts of reduced carbon for the growth of *A. hemprichii*. About half of the food that was not retained was respired, and the rest was egested, both in roughly equal rates of about 1.5 μg C/mg foram/24 h. Egestion is difficult to measure in *A. hemprichii*, because the fecal pellets do not resuspend. At present, the budget is not balanced with respect to carbon derived from feeding, because the estimated egestion is too low (ter Kuile *et al.*, 1987). To balance the budget, the egestion rate should be 12 μg C/mg C/24 h. Uptake into the skeleton was, on the average, 1.5 (1.0–2.0) μg C/mg foram/24 h (Table III). Even though uptake for photosynthesis and calcification occurs in roughly equal rates, about four times more carbon is accumulated in the skeleton than in the organic matter, because most of the photosynthates are respired. Specimens weighing less than 150 μg have higher rates of calcification than of photosynthesis, whereas specimens heavier than 3000 μg have lower rates of calcification than of photosynthesis. In the medium range, the calcification:photosynthesis ratio was constant, roughly 1:1 (comparison in Table III).

Discussion

Carbon budgets for benthonic symbiont-bearing foraminifera can best be compared to a similar budget for corals developed by Falkowski and coworkers (1984). The relative sizes of the compartments in corals and foraminifera differ: in *Amphistegina lobifera*, the symbionts, host organic matter, and skeleton contain approximately 7, 20, and 73% of the total carbon, respectively. For *Amphisorus hemprichii* these numbers are: 5, 16, and 79%. Corals contain about 1–2% organic matter (dry weight/dry weight) (Erez, 1978), which amounts to 5% of the carbon in organic form and 95% in the skeleton. The symbionts constitute only 3.7–4.5% of the total organic matter (Falkowski *et al.*, 1984), giving a final distribution of 0.2%, 4.8%, and 95% for carbon in the symbionts, host organic matter, and the skeleton.

In calcareous algae, 70–90% of the total dry weight is $CaCO_3$ (Pentecost, 1980); therefore, the ratio of carbon in the organic matter to carbon in the skeleton is about 1:1. Coccolithophores form coccoliths depending on the environmental conditions, and may shed them after formation. The relative amount of carbon in the skeleton is therefore difficult to estimate, but it is probably 1:1 as well (Sikes *et al.*, 1980; Van der Wal, 1984).

Therefore, corals contain the least amount of organic carbon per unit of inorganic (calcareous) carbon, foraminifera are intermediate, and calcareous algae contain the most. This suggests that corals need to take up fewer nutrients in the form of nitrogen or phosphorous compounds from their surroundings per unit total carbon (both organic and calcareous), foraminifera need more, and calcareous algae require still more than the symbiotic systems. This has consequences for the carbon cycling of foraminifera, because feeding may be the primary source of nutrients, at least in *A. lobifera* (ter Kuile *et al.*, 1987). Determination of feeding rates was the least reliable measurement of our budget, because feeding is a discontinuous process, and because egestion cannot be measured well. Assuming that foraminifera obtain all their nutrients from food and have the same C:N:P ratio as the food, the amount of nutrients retained can be estimated. The total daily increase of organic matter of *A. lobifera*, host and symbionts, is 1.2 μg C/mg foram/24 h, which can be provided by photoassimilation by the symbionts. The maximum feeding rate is about ten times higher. Thus, about 10% of the nutrients present in the food are retained, while almost all of the carbon derived from feeding is respired or egested (ter Kuile *et al.*, 1987). The general

"black box" observation that the efficiency of retention between trophic layers is usually around 10% further supports the validity of the high experimental rates. Based on the carbon budget, we expect that long-term feeding rates are much lower, unless feeding is very inefficient, or the feeding efficiency varies with the food concentration.

The photosynthetic rates of *Amphistegina lobifera* and *Amphisorus hemprichii* measured in this study are similar to those found by Erez (1978), but are an order of magnitude lower than those of planktonic foraminifera (Erez, 1983; Jorgensen *et al.*, 1985). Photosynthetic rates of corals, when normalized to the total weight of the organism, are similar (Erez, 1978), or much lower (Falkowski *et al.*, 1984). Total weight may not be a useful normalization factor for corals. The symbionts of foraminifera and light-adapted corals translocate sufficient reduced carbon to the host to sustain respiration and growth (Jacques and Pilson, 1980; Muscatine *et al.*, 1981, 1984; Falkowski *et al.*, 1984; Davies, 1984; Edmonds and Spencer Davies, 1986). Therefore, these systems have a potential for autotrophy with respect to carbon, but not to nutrients that must be provided by feeding (Falkowski *et al.*, 1984; ter Kuile *et al.*, 1987). Besides nutrients, planktonic foraminifera and shade-adapted corals require additional reduced carbon from feeding (Falkowski *et al.*, 1984; Jorgensen *et al.*, 1985). Excretion of mucus by corals has been well documented (Crossland *et al.*, 1980a, b; Muscatine *et al.*, 1984; Crossland, 1987), but we found no evidence that foraminifera lose photosynthetically fixed carbon in the form of mucus. Cycling of respired carbon into the skeleton has been demonstrated for both corals (Crossland *et al.*, 1980a) and foraminifera (ter Kuile and Erez, 1987).

Corals and perforate foraminifera may have another common feature, the internal inorganic carbon pool. First predicted in corals to explain the stable isotope composition of the calcium carbonate skeleton by Goreau (1977), this pool was demonstrated experimentally in perforate foraminifera, but not in imperforate species (ter Kuile and Erez, 1988). This pool functions solely as a carbon reservoir for calcification in which carbonate is concentrated in an energy-dependent process (ter Kuile *et al.*, 1989). More uptake in the pool occurs when metabolic rates supported by symbiont activity are high, but no carbon from the pool is photoassimilated (Fig 1). This correlation between uptake by the pool and photosynthetic activity may explain the lighter than expected isotopic composition of rapidly photosynthesizing corals and foraminifera (Erez, 1978). The occurrence of the same phenomenon in both classes of organisms suggests that the pool of corals may operate similarly to that of perforate foraminifera.

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